Population genetical Study of natural hybridization between Papio anubis and P. hamadryas(Dissertation_全文)

AUTHOR(S):

Shotake, Takayoshi

学位申請論文

庄武孝義

Population genetical study of natural hybridization between Papio anubis and P. hamadryas[1)]

TAKAYOSHI SHOTAKE

Kyoto University

ABSTRACT. The natural hybridization between Papio anubis and P. hamadryas in central Ethiopia was studied from a population genetical perspective. Studies were made using electrophoretical blood protein variations as markers in order to clarify the genetic relationship between them. A total of 563 samples from 10 populations which were collected in the field studies with a socioecologist in 1976 and 1979 were examined for 34 blood protein loci. Ten of the 34 loci showed polymorphism. The Tf, PA-2 and Es were found to be effective for discriminating between the anubis and the hamadryas. Genetic variability, hybridization rate, genetic distance, migration rates and correlations between genetical and morphological and between genetical and behavioral indices were computed and analyzed. The results of the present genetic survey revealed that most of the populations from which the author collected blood samples were more or less hybridized. The Nei's (1975) genetic distance between the two species was estimated to be 0.0679 at most. As this values is too small to consider these species as real biological species, it is supposed that the natural hybrid zone is fairly wide and still exapnding now.

---

1) This work was supported in part by Grants in aid for scientific research (Overseas scientific research, 1975) and of the Overseas Special Research Programme of the Primate Research Institute, Kyoto University in 1978 by Ministry of Education, Science and Culture.

INTRODUCTION

Taxonomy of the genus Papio has been in a controversy over the past 20 years (Tappen 1960; DeVore and Washburn 1963; Buettner-Janusch 1963; Jolly 1966; Roth 1965; Groves 1972; Maples 1972; Jolly and Brett 1973; Szalay and Delson 1979; Iwamoto 1980). The natural hybridization between the hamadryas baboon, Papio hamadryas and the anubis baboon, Papio anubis, considered to be clearly different species taxonomically, was discovered by Kummer et al.(1970) and Nagel (1973). In 1975 and 1978, Dr. Masao Kawai sent scientific expeditions to Ethiopia to study this natural hybridization phenomenon socioecologically. morphologically and genetically. The author took part in these expeditions to analyze the present genetic status of the hybrids. He made field surveys in central Ethiopia in the vicinity of the Awash National Park with Dr. K. Sugawara, socioecologist, under the supervision of Dr. Kawai to get genetic data over a period of 10 months. Protein electrophoresis is the most efficient technique for quantifying genetic differences between closely related species (Selander 1976) because of the selective neutrality of protein variations (Kimura 1968; Nei 1974, 1975). The author had previously studied the population genetics of Japanese macaque, Macaca fuscata, and had undertaken a systematic study of the genus Macaca using blood protein variations as a genetic marker (Shotake 1974; Shotake 1979; Shotake and Nozawa 1974; Shotake, Ohkura and Nozawa 1975; Nozawa, Shotake and Ohkura 1975; Nozawa et al. 1975, 1977, in press). He further intended to study the population genetics and taxonomy of the baboons by using the same method (Shotake, Nozawa and Tanabe 1977, Shotake 1980).

So far, some genetic variations of blood protein in the genus Papio have been reported (Buettner-Janusch 1963; Barnicot, Huehns and Dance 1965; Barnicot, Jolly and Eade 1967; Kitchin, Barnicot and Jolly 1967; McDermid, Vos and Downing 1973; Olivier, Buettner-Janusch and Buettner-Janusch 1974; Crawford and O'Rourke 1978; Lucotte 1979). However, most of these studies did not attempt to make quantitative comparison between populations or species, whereas the taxonomic status of the species in the genus Papio was in a controversy. The author published a preliminary paper dealing with the blood protein polymorphisms in Papio anubis, Papio hamadryas and their hybrid, and with estaimtes of the amount of gene exchange and the genetic distance between the two species from the data of the first expedition in 1976 (Shotake, Nozawa and Tanabe, 1977). The present paper is an extension which presents additional data and results obtained in the second expedition in 1979 and a few corrections of preliminary report.

MATERIALS AND METHODS

The field survey and blood sampling were carried out in both 1976 and 1979 at the species-border between the anubis and hamadryas baboons in the Awash Valley and on the northern edge of Awash National Park where hamadryas baboons lived south of Cassem River. Nagel (1973), Kawai and Sugawara (1976a, b), Sugawara (1979, in press) give a detailed interpretation on the hybrid zone between the anubis and hamadryas baboons. In Fig. 1 and Table 1 the places where blood sampling was carried out are indicated by alphabetical abbreviation.

AI: the anubis baboons of Ito troop

The anubis baboons which had a sleeping site in gallery

forest located 5 km above the Awash Falls (Fig. 1). This troop consisted of 73 individuals including 2 hamadryas adult males which had immigrated into this troop in 1976. However, in 1979 the size of this troop had decreased to 53 individuals including one hamadryas adult male who was different from 2 individuals observed in 1976. A total of 27 blood samples were obtained in 1976 and 1979.

AW: the anubis baboons of Welenchiti troops which lived in south-eastern part of Welenchiti Town

Thirteen blood samples were collected from the animals which had been captured by animal dealers living in Modjo Town near Addis Ababa in 1976. The place where these animals were captured was located about 15 km south-west Garibaldi Pass, where Dr Kummer (1968) saw a hybrid male and several hybrid females during his 1960 survey.

AK: the anubis baboons of Kenya

These consisted of the individuals imported by the Japan Monkey Centre from Kenya 20 years ago and their descendants. The author took 28 blood samples from these animals before leaving for 1975 expedition and had stored them in a deep freezer at -90°C.

MG: the hybrid baboons of Gorge troop

A hybrid baboon troop had a sleeping site on a cliff at 4 km below the Awash Falls (Fig. 1). This troop was intensively studied by the sociobiologist of our party and was found to consist of 63 individuals in 1976 (Sugawara, 1979). The author got 18 blood samples and some morphological data from this troop in 1976.

MK: the hybrid baboons of Kerrayu troop

A typical hybrid baboon troop had some sleeping sites on a cliff at about 10 km below the Awash Falls near Kerrayu lodge (Fig. 1). This troop which was also studied intensively by the sociobiologist and found to consist of 85 individuals (Sugawara, in press). The author got 43 blood samples and some morphological data from this troop in 1979.

HBA and HBB: the hamadryas baboons of Bassaka A and B bands

These bands sometimes joined together and made a troop in a sleeping site located on the northern edge of Lake Bassaka at the foot of Mt. Fantale. At first, it was thought that this troops was of pure hamadryas baboons, but after habituation, it was found that the troop included two adult anubis males and seven hybrid males. Thirty-nine blood samples were collected from the A band (70 individuals) and 19 from the B band (45 individuals) in 1976.

HS: the hamadryas baboons of Sabure Gorge troop

Thirty-five blood samples were collected from animals which had been captured near Sabure village and transferred to Metahara by an animal dealer in 1979.

HC: the hamadryas baboons of Cassem Gorge troops

Forty-nine blood samples were obtained from the animals which had been captured along the Cassem River and transferred to Metahara by an animal dealer in 1979.

HAG: the hamadryas baboons of Awash Game Reserve troops

These samples were collected at the stock farm of animal dealers, who caught the animals from several troops living in Awash Game Reserve located 70 km northeast from Awash Station. This was on the northern limit of the hybrid zone described by Nagel (1973) (Fig. 1). Blood sampling was carried out several times

in each population for about two months from January through March, 1976 and for about 5 months from February through July, 1979. The samples were brought to the NAMRU 5 Institute in Addis Ababa in 1976 and to a private Italian laboratory in Addis Ababa in 1979. Red cells and plasma were stored separately at -60°C in 1976 and at -25°C in 1979 until the author's departure to Japan.

Thirty-four genetic loci controlling 31 kinds of blood proteins were examined by starch and agar gel electrophoreses. They are listed in Table 2. Sampling of a protein locus was random, having no relation to whether the existence of genetic variation at this locus was likely or not. For some proteins the presence of a genetic polymorphism and the mode of inheritance in the genus Papio have already been determined [for Tf, see Buttner-Janusch (1963), Barnicot, et al. (1965) and McDermid, Vos and Downing (1973); for CA-I, see Barnicot, et al. (1965) and Barnicot, Jolly and Eade (1967) and Olivier, Buettner-Janusch and Buettner-Janusch (1974); for 6PGD and Pi, see McDermid, Vos and Downing (1973)]. The system of symbols for polymorphic loci used in this paper differs from that adopted by the above authors on account of difficulty of identification. As for the mode of inheritance of other variable proteins, codominance relations were assumed because equivalent electrophoretic bands were observed in postulated heterozygotes. At all genetic loci, the allele frequencies in individual groups could be calculated by a simple gene-counting method.

The genetic variability within populations was quantified by measuring the proportion of polymorphic loci (P_{poly}) (the criterion of polymorphism was the frequency of the commonest

alleles < 0.99); the expected proportion of heterozygotes per individual ($\bar{H} = 1 - \overline{\sum_i q_i^2}$ where q_i was the frequency of i-th allele at a locus and the average was over all loci including loci without variation); and the effective number of alleles per locus ($n_e = 1/\overline{\sum_i q_i^2}$).

From the gene frequency data, the genetic distance was calculated in every pair of the populations. The genetic distance was obtained from the normalized identity of genes as devised by Nei (1974, 1975). That is, the distance between the j-th and k-th population, D_{jk}, was calculated as $D_{jk} = - \log_e I$, where $I = \overline{\sum_i q_{ij} q_{ik}} / (\overline{\sum_i q_{ij}^2} \cdot \overline{\sum_i q_{ik}^2})^{\frac{1}{2}}$. In the formulae I was the normalized identity of genes (genetic similarity), q_{ij} and q_{ik} were the frequencies of the i-th alleles at a locus in the j-th and k-th populations, respectively, and the averages were over all the gene loci examined including loci without variation.

RESULTS

Description of blood protein polymorphism

Of the 34 genetic loci examined 10 loci, that is, Tf, Pi, PA-2, Plasma Es, 6PGD, PGM-I, PGM-II, ADA, CA-I and AK showed polymorphism. In the previous report (Shotake, Nozawa and Tanabe, 1977) TBPA locus was polymorphic, but it was clarified by the succeeding examination that this locus was completely monomorphic. This locus was not therefore used for genetic analysis in the present work. The author found a new allele in PA-2 locus in the present study. The patterns of the electrophoretic variations are shown in Fig. 2. Table 3 gives the frequencies of different alleles occurring at each locus in the 10 populations of baboons. Detailed interpretations of these variable loci are as follows.

Tf (Plasma transferrin):

The author found eight kinds of genotypes, that is DD, DD', D'D', D'E, DE, EE, D'C and EC controlled by four alleles at this locus among the hamadryas baboons, the anubis baboons and their hybrids. The mobility difference between D and D' alleles was slight and it was sometimes difficult to distinguish the genotypes D'D, DD or D'D'. But this problem could be solved by running the samples side by side on electrophoresis. The hamadryas baboons had two alleles, D and E. These alleles seemed to correspond to S and F alleles, respectively, which Barnicot, Huehns and Dance (1965) had found in the hamadryas baboons. The anubis baboons had the alleles C, D' and E. These corresponded probably S, M and F alleles, respectively, of the yellow baoons (Papio cynocephalus) as reported by Barnicot, Huehns and Dance (1965), and to the A, B and C or 3, 2 and 1 alleles, respectively described by Buettner-Janusch (1963, 1965), to the A, B and C alleles, respectively, of chacma baboons (Papio ursinus) as reported by McDermid, Vos and Dowing (1973), and to the S, M and F alleles, respectively, of the guinea baboon (Papio papio) of Lucotte and Guillon (1979).

Several researchers investigated the Tf locus of Chaeropithecus baboons, but, with the exception of Barnicot, et al. (1965), they could not find the allele corresponding to our D allele in the hamadryas baboons. Also, in the present work, the D allele could not be found in the anubis populations AK and AI. The author found the D allele with a low frequency in AW group, but it was probable that this group had been hybridized with the hamadryas as described in Materials. It was inferred that the D allele did not exist in the anubis and that the D'

allele did not exist in the hamadryas, because the frequency of D' allele was very high in the anubis groups AK, AI and AW, but very low in the hamadryas groups HBA, HBB, HS, HC and HAG. Crawford and O'Rourke (1978) reported that there were only two alleles in the hamadryas baboons housed at the Sukhumi Center, USSR. The D' allele in HBA, HBB, HS, HC and HAG would thus be the result of the migration of anubis genes from outside.

Pi (Plasma protease inhibitor or α_1-antitrypsin):

The author found three alleles and four genotypes at this locus (Fig. 2). As the anubis populations were completely monomorphic and the variants were observed in the hamadryas and hybrid populations only, it was inferred that the variant allele N and Q had originated from the hamadryas populations. McDermid, Vos and Dowining (1973) reported two alleles in the chacma baboons, but the author could not compare the mobilities of their alleles with ours.

PA-2 (Plasma prealbumin-2):

Barnicot, Huehns and Eade (1965) reported that there were two alleles at this locus, but the present author found three alleles and 6 phenotypes. The phenotypes with the fast, middle, slow and double bands were assumed to correspond to the genotypes, 1-1, 2-2, 3-3, 2-1, 3-1 and 3-2, respectively (Fig. 2). The 2 allele was observed to have high frequencies in AK and AI populations which were considered to be pure anubis, while the other populations displayed polymorphism. The frequency of the 1 allele was about 75% in the hamadryas groups HBA, HBB, HS, HC and HAG. This locus is thus considered as an effective locus for

discriminating between the anubis and the hamadryas populations.

Es (Plasma esterase):

This plasma esterase was considered to exist in the A zone of Barnicot, Huehns and Eade (1965). The author found two esterase bands in the plasma prealbumin area by using the Shaw and Prasad's (1970) method. The phenotypes with the fast, slow and double bands were considered as expressions of the genotypes F, S and FS, respectively (Fig. 2). The S allele was apparently at fixation in the AK and AI populations (considered to be pure anubis), but the hamadryas populations exhibited high polymorphisms with about fifty-fifty gene frequencies. This locus was also an effective locus for discriminating between the anubis and hamadryas populations.

6PGD (Red cell 6-phosphogluconate dehydrogenase):

The author found a variant band with a slightly slower mobility than the common bands. The common phenotype being E, the variant phenotypes were named as EF and F (Fig. 2). McDermid, Vos and Dawning(1973) also found a variant allele in the chacma baboons, but this variant allele seemed to be different from the one found by the present author judging from their mobility. The pure anubis groups did not have the variant, but the hybrid and hamadryas groups were polymorphic.

PGM (Red cell phosphoglucomutase):

It might be thought that the Papio PGM were controlled by two genetic loci, PGM-I and PGM-II, as in other primate species (Shotake, Ohkura and Nozawa, 1975). However, the isozymes

controlled by the PGM-I and PGM-II loci appeared at rather more separate positions than those of other primates on electrophoresis. The author found that the PGM-I locus was polymorphic in the anubis baboon, while the PGM-II locus was variable even in the hamadryas baboon (Fig. 2)

ADA (Red cell adenosine deaminase):

The common ADA type seemed to be controlled by the normal allele 2 and the variant type with a faster band by the other allele 4 (Fig. 2). The anubis population from Kenya, AK, was polymorphic at this locus. The author found some variant alleles in HAG, HS and HC groups and it was postulated that the variants had been brought into these groups by immigrants carrying the anubis genes.

CA-I (Red cell carbonic anhydrase):

The variant allele found by the present author was considered to be identical with the b allele found by Barnicot, Jolly and Eade (1967) (Fig. 2). As the allele b was observed in AK, AW and HAG populations, the variant could have originated from the anubis populations.

AK (Red cell adenylate kinase):

A variant at this locus was observed in four hamadryas and one anubis groups. We postulated that this variant was a 2-1 heterozygote (Fig. 2).

We could not find any remarkable polymorphism at the red cell enzyme loci. The Tf, PA-2 and Plasma Es loci, however, were

useful for to genetically differentiating baboon populations. In that respect, it was found that the genus Papio differed from the genera Macaca (Nozawa et al., 1975; Nozawa et al., 1977; Shotake, 1979), Cercopithecus (Kawamoto, unpublished data) and Theropithecus (Shotake, 1980).

Estimations of hybridization rate

Genetical estimation of the hybridization rate between the anubis and hamadryas was one of the most interesting problems. In considering this, the Tf locus was the best genetic marker, because the anubis had the C, D' and E alleles while the hamadryas had the D and E alleles (Table 3). The hybridization rate can be calculated by the following formula,

$$M = \frac{q_1 - q_o}{Q - q_o} \quad \text{(Glass and Li, 1953)}$$

where M is the hybridization rate, q_o the frequency of D' allele in the non-hybridized population which was zero, q_1 the frequency of D' allele in the hybridized population, and Q the frequency of D' allele in the anubis population. The hybridization rates of the MG and MK populations were calculated as

$$M_{MG} = \frac{0.6667 - 0}{0.8846 - 0} = 0.7537 \quad \text{and}$$

$$M_{MK} = \frac{0.2907 - 0}{0.8846 - 0} = 0.3286,$$

respectively; that is, it can be considered that 75.4 % and 32.9 % of the genes in the MG and MK populations, respectively, have originated from the anubis. Here, we used to the value of 0.8846 for Q. That is because Buettner-Janusch (1963, 1965) reported the existence of an allele corresponding to our E allele in Kenya and because the AI population in our study contained 7 % E and 4 % C alleles. The estimated hybridization rates of the

other populations from the anubis population are given in Table 4. In addition, the hybridization rate was estimated using the polymorphisms at PA-2 and Es loci and calculating the average rate of hybridization for the Tf, PA-2 and Es loci (Table 4). In these cases,the values of 0.2394 and 0.6083 were assigned to q_o for the 2 allele at the PA-2 and the S allele at the Es loci, respectively, these being the average among the 5 hamadryas populations. As the estimation of a hybridization rate for AW group by the D' allele was very difficult, the hybridization rate was estimated by the penetration rate of D allele into AW group instead. In this case, Q was assigned a value of 0.1538, this being the frequency of the D allele in HBA group (apparently the purest hamadryas group). The penetration rate for the AW group was calculated as

$$M_{AW} = \frac{0.0385 - 0}{0.1538 - 0} = 0.2567,$$

and 1 - 0.2567 = 0.7433 is given in Table 4 as the hybridization rate of AW group.

Quantification of genetic variability within population

The genetic variabilities of each population are also shown in Table 4. The proportion of polymorphic loci, P_{poly}, of the MG, MK, HS, HC and HAG groups which were invaded more or less by anubis genes were higher than those of the three anubis groups AK, AI and AW. The average heterozygosity per individual, $\bar{H}$, in the pure anubis groups AK and AI was less than 0.03. This is smaller than those of the hamadryas groups, but larger than those ($\bar{H}$ = 0.013) of gelada baboons (Theropithecus gelada), in the central Ethiopian highland (Shotake, 1980). It is natural that the genetic variability of the AK groups should be small,

since this group has been kept in an enclosure for 20 years ago. The $\bar{H}$ value of the hamadryas groups HBA and HBB (apparently almost pure hamadryas) was 0.0407 on average, and this is higher than that for the anubis (AK and AI). The fact that the MG and MK groups had the highest $\bar{H}$ values, 0.0526 and 0.0529, respectively, might suggest that the hybridization was secondary intergradation. Generally speaking, the genetic variability of the genus Papio estimated in the present work was rather less than those for the genus Macaca (Nozawa et al., 1977).

Estimation of genetic distance between populations

The genetic similarity and genetic distance between the populations of baboons were calculated by the Nei's (1975) method. Matrices of genetic similarity and genetic distance are presented in Table 5. The average genetic distance between the anubis groups was 0.0041 and that between the hamadryas groups was 0.0024. These values approximate those between troops of Japanese macaque (Nozawa et al., 1975) and between herds of gelada baboons (Shotake, 1980). The average genetic distance between the anubis and hamadryas groups was calculated as 0.0451. This value was slightly higher than the value between Japanese mainland macaque (Macaca fuscata fuscata) and Japanese Yaku macaque (Macaca fuscata yakui), and was only a third of the average genetic distance between species of the genus Macaca, which was 0.1385 (Nozawa et al., 1977). However, the genetic distance between the anubis and hamadryas baboons estimated in this work is probably an underestimate, because most of the baboon populations from which the author collected blood samples were considered to contain genes from both the anubis and hamadryas baboons. The author, then, attempted to estimate

genetic distance between the pure anubis and hamadryas baboons by Nei's (1972) formula which corrects the genetic distance between the hybrid populations by the hybridization rate. That is,

$$\begin{bmatrix} J_{XO} \\ J_{XYO} \\ J_{YO} \end{bmatrix} = (1-p-q)^{-2} \begin{bmatrix} (1-q)^2 & -2p(1-p) & p^2 \\ -q(1-q) & (1-p-q+2pq) & -p(1-p) \\ q^2 & -2(1-p)q & (1-p)^2 \end{bmatrix} \begin{bmatrix} J_X \\ J_{XY} \\ J_Y \end{bmatrix}$$

and $I_O = J_{XYO}/(J_{XO}\, J_{YO})^{\frac{1}{2}}$, $D_O = -\ln I_O$,

where p is the proportion of genes in population X that comes from population Y, and q the proportion of genes in Y that comes from X, and J_{XO}, J_{XYO} and J_{YO} are the identity of genes corresponding to J_X, J_{XY} and J_Y, respectively, before hybridization occurred. I_O and D_O are the genetic similarity and distance, respectively, before hybridization. The corrected genetic distances between the anubis and hamadryas populations are given in parentheses in Table 5. The average corrected genetic distance between the anubis and hamadryas groups was calculated as being 0.0679. This value coincided well with that obtained between the "pure" species inferred in our previous report (Shotake, Nozawa and Tanabe, 1977).

The genetic distances between the hybrid population MG and the anubis groups were smaller than those between the MG and the hamadryas groups, whereas the genetic distances between the hybrid population MK and the hamadryas groups were smaller than those between the MK and the anubis group. Figure 3 is the dendrogram drawn from the genetic distance matrix of Table 5 by using the unweighted-pair-group method (Sokal and Sneath, 1963). It can be concluded from Fig. 3 that the MG population had a closer relationship with the anubis than with the hamadryas

baboon, whereas the MK population had closer relationship with the hamadryas baboon. This view is supported by the calculated hybridization rates (Table 4). The AW population was closer to the anubis than the MG population, though AW population had a hybridization rate equal to that of MG population (Table 4).

Correlations between morphological and genetical hybrid indices and between rank orders of genetical index and behaviour.

Sugawara (1979, in press) carried out an intensive ecological and sociological survey on the MG and MK groups and determined a morphological hybrid index for each individual belonging to these hybrid groups. I attempted to test the correlation between the genetical index measured by the protein markers and both of the morphological index and the rank order of behaviour given by Sugawara (1979, in press) in order to investigate a detailed status of hybrid group. Table 6 shows the morphological and genetical hybrid indices and the rank order of behaviour in each individual from which blood samples was collected. The morphological hybrid index was determined by Sugawara (1979) as follows: eight morphological characters with a clearly different appearance in anubis and hamadryas males were selected. Each character was given score 0 for hamadryas appearance, score 1 for intermediate appearance and score 2 for anubis appearance. The morphological hybrid index of each male is the sum of these eight scores. The rank order of males was defined by Sugawara (1979) as the arrangement according to their tendency to herd females. The genetical hybrid index was calculated by the following procedure. Three loci (Tf, PA-2 and Es) for discriminating between the anubis and the hamadryas were used. Each allele at these loci was basically given score 0 for hamadryas

type and score 1 for anubis type but some corrections were added for allele frequencies; for the Tf locus, alleles D', C, E and D were given scores 1, 1, 0.1 and 0, respectively, because the anubis populations had 10% E allele: for Es locus, alleles S and F were given scores 0.5 and 0, respectively, because 50% S allele was existing in hamadryas populations: for the PA-2 locus, alleles 2, 1 and 3 were given 0.9, 0 and 0, respectively, because 10% 2 allele was exsiting in hamadryas populations. The genetical hybrid index of each male is the sum of three genotype scores calculated from the allele scores (Table 6). The correlation coefficients between the three loci, between the genetical and morphological indices and between the rank orders of genetical index and behaviour are given in Table 6. The correlation coefficients among the three loci were approximately zero, suggesting that there were no linkage disequilibrium in these populations and that these populations had passed through many generations since the beginning of hybridization. The correlation coefficients between genetical and morphological hybrid indices showed relatively high values for each locus though statistically not significant in MG group, but non-significant negative values in MK group. Also, rank correlations between rank orders of genetical index and behaviour in MG group showed relatively higher value though statistically not significant than in MK group. Several of the animals in the MG group appeared to be anubis individuals which may have immigrated directly into this group from nearby anubis troops. If so, it is likely that these animals have elevated the correlations coefficients between the genetical and morphological hybrid indices and between rank orders of genetical index and behaviour.

Also, this phenomenon may suggest that the MG group is the anubis population which has more recently been hybridized by the gene flow from the hamadryas baboons.

Migration rates among heighbouring populations

Next, the migration rate between neighbouring troops of the hamadryas, the anubis and the hybrid were estimated. Wright (1965) derived a formula giving the functional relationships between F_{ST} (inbreeding coefficient due to population subdivision) and m (migration rate per generation) on the assumption of island model of population structure, namely,

$$F_{ST} = \sigma_q^2 / \bar{q}(1 - \bar{q}) = \frac{(1 - m)^2}{2N - (2N - 1)(1 - m)^2}$$

where q and σ_q^2 stand for the mean and variance, respectively, of frequencies of an allele at a variable locus among populations, and N is the effective size of subpopulation. From this formula, we can estimate the average migration rate ($\bar{m}$ per generation) by the following equation:

$$\bar{m} = 1 - \sqrt{\frac{2\bar{N}\,\bar{F}_{ST}}{(2\bar{N} - 1)\,\bar{F}_{ST} + 1}}$$

The author could estimate approximately the effective population size of hamadryas baboons as a half of its census size by the following procedure. Nozawa (1972) devised a simple formula by which the effective population size of Japanese monkey troops could be estimated. That is,

$$N = \frac{2N_c(N_c - 1)}{\sum_i k_{mi}^2 + N_c^2 / N_f - N_c}$$

where N is the effective population size, N_c the census number of population, N_f the census number of adult females and $\sum_i k_{mi}^2$ the sum of squares of the number of gamates contributed by the individual male parents. Assuming that this formula is applicable to the baboon populations, we can estimate $\sum_i k_{mi}^2$ in the hamadryas population by examining the composition of troops or bands, because a hamadryas troop or band consists of a number of one male units (Kummer, 1968). The author could examine the composition of HBA and HBB bands by the field survey in 1976 and calculated the approximate $\sum_i k_{mi}^2$ values by the number of one male units and the number of females belonging to them as shown in Table 7, assuming that a leader male has an equal chance to contribute offspring to the next generation by mating with his accompanying females in his own unit. As a result, it was found that the effective population size was approximately a half of the census size in the hamadryas band. Kummer (1968) described that the proportion of adult males and females were on average 18.0 and 32.4%, respectively, of the census number of the hamadryas populations. The effective population size can be roughly estimated using these values and the Wright's formula (1938), $N = 4N_mN_f / (N_m+N_f)$, that is, $N = 4 \times 0.18N_c \times 0.32N_c / (0.18N_c + 0.32N_c) = 0.46N_c$. Thus, we can again say that the effective population size of the hamadryas baboons is approximately a half of the census size. Also, we could estimate the effective population size of anubis baboons as one third of its census size according to Nozawa's (1972) method, because the social structure of anubis baboons is similar to that of Japanese macaques, Macaca fuscata,

and assume that the effective population size of hybrid groups was a value between one third and a half of their census size allocating proportionally their hybridization rates.

The average effective size ($\bar{N}$) of two or three neighbouring troops can be obtained from the harmonic means of the N's. Table 8 gives the results of estimation of migration rate between neighbouring bands and troops of hamadryas baboons and between neighbouring troops of anubis and hybrid baboons. Here, the commonest allele frequency at each locus was used for q. The average migration rate ($\bar{m}$) between A and B bands in the HB troop shows the highest value and this is comparable with that obtained among three troops which occurred by fission (Sugiyama 1960, Kano 1964) from one troop of Japanese macaques, Macaca fuscata, at Takasakiyama (Nozawa et al., in press). Nozawa et al. (in press) suggested that the $\bar{m}$ values obtained from several loci should be considered as underestimates, because the variance of the commonest allele frequencies (σ^2_q) contains a sampling variance. Consequently, it should probably be concluded that the neighbouring three troops of hamadryas baboons, HB, HS and HC, are exchanging individuals at a migration rate of rather more than 12% per generation. Assuming the genetic equilibrium in the species border and hybrid zone, the migration rates between the two neighbouring groups MG and MK and between hybrid group MG and anubis troop AI were roughly estimated as about 0.0750 and 0.0139 per generation, respectively (Table 8).

DISCUSSION

Genetic variability ($\bar{H}$: average heterozygosity per individual) of an anubis baboon troop was about 0.02 and that was smaller than 0.04 obtained in a hamadryas baboon troop (Table 4). Lucotte (1979) reported that heterozygosities ($\bar{H}$) in four baboon species, Papio papio, P. anubis, P. cynocephalus and P. hamadryas were 0.039, 0.018, 0.028 and 0.05, respectively. Olivier, Buettner-Janusch and Buettner-Janusch (1974) found two polymorphisms only at the CA loci of olive baboon, Papio anubis , living in the Laipikia district of northern Kenya. It is a somewhat surprising that despite the anubis baboons, Papio anubis, have the widest distribution of the genus Papio, they have maintained a relatively smaller variability compared with the more peripheral species. Nozawa, Shotake and Ohkura (1975) and Nozawa et al. (1975) suggested that genetic drift could be a cause of low genetic variability ($\bar{H}$ = 0.014) within, and marked differentiation between, troops of the Japanese macaque, Macaca fuscata. Shotake (1980) also considered that bottle-neck effect would diminish the genetic variability of gelada baboon, Theropithecus gelada, ($\bar{H}$ = 0.013) as a result of a reduction of the population. Genetic drift or bottle-neck effect may be invoked to interpret low genetic variability of the anubis baboons, since their population structure is similar to that of Japanese macaques (Kawai and Sugawara, 1976a,b) and Kawai and Sugawara (1976a,b) suggest that this species has rapidly expanded its distribution area and population size. But, there is at present no evidence available to test the validity of this hypothesis.

Most of the baboon populations from which the author

collected blood samples were considered to contain genes from both the anubis and hamadryas baboons (i.e., most of them were more or less hybrid populations). The habitat of the HAG troops was more than 70 km away from the hybrid zone described by Nagel (1973) in the Awash Valley. The HC and HS troops also lived in the gallery forest along the Cassem river located more than 30 km away from the Awash Valley, while the HBA and HBB bands lived 30 km away from the western edge of the valley. The distribution area of these populations were located in the area which was indicated as the habitat for pure hamadryas by Nagel (1973). The AW troop was located 15 km away from the Garibaldi pass which Nagel (1973) indicated as the western edge of hybrid zone. This suggests that the hybrid zone between P. anubis and P. hamadryas is not as narrow as originally thought. Field surveys undertaken by Kawai and Sugawara (1976a, b) and by Iwamoto (1980) in south-east Ethiopia led them to argue that the hybrid zone extended over an area of about 300 x 300 km^2, including the border between Ethiopia and Somalia.

In 1976, we observed that two hamadryas adult males had penetrated into the anubis troop AI and mated with several anubis females. Therefore, we expected in 1979 expedition that we would find many hamadryas genes there; however, we could find few typical hamadryas genes such as D and F alleles at the Tf and P-Es loci, respectively, and could not completely prove that gene flow from hamadryas to anubis had occurred in this hybridization zone as well as that from anubis to hamadryas. However, as we found E and 1 alleles at the Tf and PA-2 loci, respectively, which might come from the hamadryas, the possibility of direct gene flow from hamadryas to anubis was not necessarily excluded. Although gene flow around the border between anubis and hamadryas

habitats would mainly be caused by the migration of the anubis females kidnapped by the hamadryas males into the hamadryas troops as postulated by Nagel (1973), we could not explain the formation of the MG group which consisted of almost pure anubis genes only by one way gene flow. It seems more likely that the hybridization of anubis troops by the hamadryas have been accomplished gradually by hybrid baboons who could adapt to the environment of anubis baboons more easily. Although we consider that the speed of infiltration of hamadryas gene is slower than that of anubis genes, our surveys suggest that hybrid individuals of every grade between the two species of baboons are found in our study area. Then, it appears that the hybrid zone between the anubis and hamadryas baboons is still expanding now. Although Nagel (1973) argued that an evolutionary approach to the species problem should consider reproductive isolation between populations in terms of not only interbreeding (Mayr's (1963) definition), but gene flow (Bigelow's (1965) definition), Szalay and Delson (1979) described by only Mayr's definition without considering gene flow that Papio anubis and P. hamadryas were subspecies within a species. Our results show that there is no reproductive isolation between the two baboons species and this hybridization phenomenon suggests by Bigelow's (1965) definition that they probably are subspecies within a species.

Nei (1975) has shown that the genetic distance between local races within species was in the range of 0 ~0.0058, and between species within genera in the range of 0.5 ~2.5. Our estimation of genetic distance between local populations of the hamadryas and of the anubis approximated to the Nei's range of distance between local races. However, the average genetic distance between the anubis and hamadryas corrected for

hybridization rate was 0.0679 and this value was less than one tenth of the distance between species. This value was about a half of the average genetic distance between species of the genus Macaca (namely, 0.1385: Nozawa et al., 1977). Lucotte (1979) calculated the genetic similarity among four Papio species, Papio papio, P. anubis, P. cynocephalus and P. hamadryas by using 14 loci and got values of 0.94 between P. hamadryas and the other three species and about 0.96 among the three species except P. hamadryas. Genetic distances (0.062 and 0.040, respectively) estimated from these values dropped below the lower limit of the Nei's genetic distance between subspecies. We estimated the average genetic distance among three genera of Cercopithecidae, Papio, Macaca and Cercopithecus, as about 0.65 (Kawamoto et al., 1977, Shotake 1978) and Shotake (unpublished data) estimated it as about 0.60 between Theropithecus and Papio. These values were close to the lower limit of the distance between species. We had already suggested that the classification of Asian macaques should be reconstructed by lowering so-called genus to species rank and so-called species to subspecies rank (Nozawa et al., 1977). Here, again, we have to support Grove's (1972), Brett et al.'s (1976) and Szalay and Delson's (1979) suggestions that the subgenus Chaeropithecus could be considered as a single species bearing the species name Papio hamadryas Linnaeus 1758. On the other hand, an alternative opinion is that the hamadryas is one species, Papio hamadryas, (Kawai and Sugawara, 1976a, b; Iwamato, 1980) and other Papio species should be lumped into another species, Papio cynocephalus (DeVore and Washburn, 1963; Buettner-Janusch, 1966; Jolly, 1966; Kingdon, 1971). This opinion is based largely on the morphological

differences between the adult males and on the differences in social structure between the hamadryas and the other Papio "species".

The genetic distance of 0.0679 suggets that a divergence time between the hamadryas and anubis can be calculated as 339,500 years (using Nei's [1975] method). Since the divergence time estimated from genetic distances in the Asian macaques was relatively comparable to palaeontological estimation (Nozawa et al., 1977), we infer that a population of the common ancestors of the Papio baboons were cut off in a dry area in the north-eastern part of Africa during the middle Pleistocene and were exposed to such intense selection pressure in a hot and dry environment that their morphology and behaviour differentiated rather rapidly. Considering that the morphological differences between Negroid and Mongoloid peoples in Homo sapiens have been established only for about 120,000 years (Nei, 1975), our conjecture is not so unreasonable. If the fossils of Papio sp. found at Hadar (Johanson and Taieb, 1976) and Omo (Eck, 1977 and Iwamoto, personal communication) in Ethiopia prove to be from the common ancestors of the present Papio species, it would lend considerable support to our hypothesis.

Sugawara (1979, in press) reported that there were significant correlations between the rank order with which males tended to herd females and their morphological rank order (hybrid indices) from hamadryas to anubis in both the hybrid groups MK and MG and suggested that the behaviour of hamadryas adult males was controlled by a genetic factor. In contrast, there are few correlations between morphological and genetical indices in the present analyses, perhaps because the genetical index is calculated only from three major genes as markers and

these major genes may have continued to segregate and recombine independently of the morphological characters through several generations after hybridization. Moreover, we can not identify any significant correlations between the behaviour of hamadryas adult males and their possession of the three major genes. It seems likely that the lack of these correlations are because the morphological and behavioural characters observed by Sugawara are controlled by polygenic factors segregating independently with each other.

Olivier, Buettner-Janusch and Buettner-Janusch (1974) attempted to estimate the migration rate per generation ($\bar{m}$) among nine troops of anubis baboons inhabiting in Laipikia district in northern Kenya by using two polymorphic loci of carbonic anhydrase as markers. They estimated $\bar{m}$ at the range from 0.094 to 0.214 corresponding to N (effective population size) varying from 85 to 30, respectively. The author's estimate of average migration rate ($\bar{m}$) among three troops of hamadryas baboons was 0.12 and this would seem to be comparable to those obtained among the anubis troops studied by Olivier, Buettner-Janusch and Buettner-Janusch (1974), the distribution area of the troops being approximately equal and the effective population sizes being in a same range. Assuming a genetic equilibrium in the hybrid zone, the migration rate between the two neighbouring hybrid group MG and MK was roughly estimated as about 0.075 per generation and this value was considered to be compatible with the results of field observation suggesting that MG and MK groups had exchanged at least a few individuals during the last three years (Sugawara, in press). Thus, we can conclude that there is much migration between troops of baboons and that

the migrant genes from one kind of baboon have been diffusing into the populations of the other kinds.

ACKNOWLEDGEMENTS

The author wishes to express his thanks to Dr. Ken Nozawa and Dr. Masao Kawai for encouraging and supervising this work. Thanks are due to Dr. Mitsuo Iwamoto, Dr. Umeyo Mori, Dr. Hideyuki Ohsawa, Dr. Kazuyoshi Sugawara, Dr. Yuichi Ono and his team at Faculty of Science, Kyushu University, for their valuable help during research expedition and Mr. Yoshi Kawamoto and Miss Yoshiko Ohkura and Miss Atsuko Ohno for their technical assistance and in preparing this manuscript. The author thanks also Dr. Robin I. M. Dunbar for his valuable comments to the English expression of this manuscript. The author thanks also Drs. Douglas Obeck and Owen Wood of the NAMRU 5 Institute of the United States of America and Mr. Guilio Tartaglia who kindly offered laboratory and freezer facilities for storing blood samples. The author is also indebted to the following for their cooperation: Messers Techiome Ashine, Lealem Berhanu, Hagos Yohannes, Taddesse Gabre-Michaiel, Ande-Berhanu Kidane, Tesfaye Wundesa, Akinori Mizuno and Mikio Kaji of the Ethiopian Wild life Conservation Organization; Dr. Shibur Tedla and Mrs. Misrak Elias of Addis Ababa University: His Excellency Ambassador Mitsuo Hashizume and Messers Toshiaki Takahashi, Yuji Harada and Kuniyoshi Ohta of the Embassy of Japan to Ethiopia; Messers Sadanori Taguchi and Yasushi Inaba of Japan Overseas Cooperation Volunteer, and the members of the Japan Monkey Centre.

REFERENCES

Barnicot, N. A., C. J. Jolly, E. R. Huehns and N. Dance, 1965. Red cell and serum protein variations in baboons. In "The Baboon in Medical Research" (H. Vagtborg, ed) Univ. of Texas Press, Austin, Vol. 1, pp.323-338.

Barnicot, N. A., C. J. Jolly and P. Eade, 1967. Protein variation and primatology. Amer. J. Phys. Anthrop., 27: 343-356.

Baur, E. W. and R. T. Schorr, 1969. Genetic polymorphism of tetrazolium oxidase in dogs. Science, 166: 1524-1525.

Bigelow, R. S., 1965. Hybrid zones and reproductive isolation. Evolution, 19: 449-458.

Brett, F. L., C. J. Jolly, W. W. Socha and A. S. Wiener, 1976. Human-like ABO blood groups in wild Ethiopian baboons. Yearbook of Physical Anthorpology, 20: 276-289.

Buettner-Janusch, J., 1963. Hemoglobins and transferrins of baboons. Folia Primat., 1: 73-87.

Buettner-Janusch, J., 1965. Biochemical genetics of baboons in relation to population structure. In "The Baboon in Medical Research" (H. Vagtborg, ed.) Univ. of Texas Press, Austin, Vol. 1, pp.95-110.

Buettner-Janusch, J., 1966. A problem in evolutionary systematics: nomenclature and classification of baboons, genus Papio. Folia. Primat., 4: 288-308.

Crawford, M. H. and D. H. O'Rourke, 1978. Inbreeding, Lymphoma, Genetics and Morphology of the Papio hamadryas Colony of

Sukhumi. J. med. Primatol., 7: 355-360.

DeVore, I. and S. L. Washburn, 1963. Baboon ecology and human evolution; In "African Ecology and Human Evolution" (F. C. Howell and F. Bourliere ed.) Aldine Publishing, Chicago., pp.335-367.

Eck, G., 1977. Diversity and frequency distribution of Omo Group Cercopithecoidea. J. Hum. Evol., 6:55-63.

Glass, B. and C. C. Li, 1953. The dynamics of racial intermixture —an analysis based on the American Negro. Amer. J. Human Genetics, 5: 1-20.

Groves, C. P., 1972. Phylogeny and calssification of primates; In "Pathology of Simian Primates" (Fiennes, ed.) Karger, Basel., part I, pp.11-57.

Hopkinson, D. A., M. A. Mestriner, J. Cortner and H. Harris, 1973. Esterase D: a new human polymorphism. Ann. Hum. Genet., 37: 119-137.

Ishimoto, G., 1972a. Blood protein variations in Asian macaques. I. Serum proteins and hemoglobin. J. Anthrop. Soc. Nippon, 80; 250-274. (in Japanese)

Ishimoto, G., 1972b. Ibid. II. Red cell enzyme. J. Anthrop. Soc. Nippon, 80: 337-350. (in Japanese)

Ishimoto, G., M. Kuwata and T. Shotake, 1973. Polymorphism of red cell NADP-dependent isocitrate dehydrogenase in macaque monkeys. J. Anthrop. Soc. Nippon, 82: 52-58.

Ishimoto, G., M. Kuwata and T. Shotake, 1975. A variant hemoglobin found in Macaca fuscata: Another polymerizing hemoglobin of macaques. J. Anthrop. Soc. Nippon, 83: 233-243.

Imlah, P., 1964. Inherited variants in serum ceruloplasmin of the pig. Nature, 203: 658-659.

Iwamoto, M., 1980. On the distribution of baboons in Ethiopia. J. Anthrop. Soc. Nippon, 88: 387-396. (in Japanese)

Johanson, D. C. and M. Taieb, 1976. Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. Nature, 260: 293-397.

Jolly, C.J., 1966. Introduction to the Cercopithecoidea, with notes on their use as laboratory animals. Symp. Zool. Soc. London, 17: 427-457.

Jolly, C. J. and F. L. Brett, 1973. Genetic markers and baboon biology. J. Med. Prim., 2: 85-99.

Kano, K., 1964. On the second fission of natural troop of Japanese monkey in Takasakiyama. In: Japanese Monkeys in Takasakiyama, Keiso Shobo, Tokyo, pp. 42-73. (in Japanese)

Kawai, M. and K. Sugawara, 1976a. Hybridization and evolution of primates. I. Social structure of hybrid baboon group between Papio anubis and Papio hamadryas. Shizen, 31(11):48-57. (in Japanese).

Kawai, M. and K. Sugawara, 1976b. Ibid. II. Speciation and hominization. Shizen, 31(12):64-73. (in Japanese)

Kawamoto, Y., T. Shotake, Y. Ohkura, K. Nozawa and Y. Tanabe, 1977. Genetic variability among 3 genera of Cercopithecidae. Japan. J. Genetics, 52: 451. (abstract) (in Japanese)

Kimura, M., 1968. Evolutionary rate at the molecular level. Nature, 217: 624-626.

Kingdon, J., 1971. East African mammals. "An Atlas of Evolution in Africa." Vol. I. Academic Press, London and New York.

Kitajima, M., Y. Ohkura, T. Shotake and K. Nozawa, 1975. Genetic polymorphisms of blood proteins in the troops of Japanese macaques, Macaca fuscata. IV. Erythrocyte esterase polymorphism in Macaca fuscata. Primates, 16: 399-404.

Kitchin, F. D., N. A. Barnicot and C. J. Jolly, 1967. Variations in the group-specific component (Gc) and other blood proteins of baboons: In "The Baboon in Medical Research" (H. Vagtborg,

ed.) Univ. of Texas press, Austin., Vol. 2, pp.636-657.

Kummer, H., 1968. Social organization of hamadryas baboons. Bibliotheca Primatologica, No.6, S. Karger, Basel.

Kummer, H., W. Goetz and W. Angst, 1970. Cross-species modification of social behavior in baboons: In "Old World Monkeys, Evolution, Systematics and Behaviour" (J. R. Napier, and P. H. Napier, ed.) Academic Press, London, pp.351-363.

Lucotte, G., 1979. Génétique des populations, spéciation et taxonomic chez les babouins: II. Similitudes génétique comparées entre différentes espéces: Papio papio, P. anubis, P. cynocephalus et P. hamadryas basées sur les données du polymorphisme des enzymes erythrocytaires. Biochem. Syst. Ecol., 7: 245-251.

Lucotte, G. and R. Guillon, 1979. Ibid: I. Polymorphisme electrophorétique des proteines et enzymes rériques chez le babouin de Guinée, Papio papio. Biochem Syst. Ecol., 7: 239-244.

Maples, W. R., 1972. Systematic reconsideration and a revision of the nomenclature of Kenya baboons. Amer. J. phys. Anthrop., 36: 9-20.

Mayr, E., 1969. Principles of systematic zoology. McGraw-Hill, New York.

McDermid, E. M., G. H. Vos and H. J. Downing, 1973. Blood groups, red cell enzymes and serum proteins of baboons and vervets. Folia Primat., 19: 312-326.

Nagel, U., 1973. A comparison of anubis baboons, hamadryas baboons, and their hybrids at a species border in Ethiopia. Folia Primat., 19: 104-165.

Nei, M., 1974. A new measure of genetic distance. In "Genetic distance" edited by J. F. Crow, Plenum, New York, pp.63-76.

Nei, M., 1975. "Molecular Population Genetics and Evolution." north-Holland, Amsterdam and Oxford.

Nozawa, K., 1972. Population genetics of Japanese monkeys: I. Estimation of the effective troop size. Primates, 13: 381-393.

Nozawa, K., T. Shotake and Y. Ohkura, 1975. Blood protein polymorphisms and population structure of the Japanese macaque, Macaca fuscata fuscata. Isozymes IV. Genetics and Evolution, C. L. Markert ed. Academic Press, New York, pp.225-241.

Nozawa, K., T. Shotake, Y. Ohkura, M. Kitajima and Y. Tanabe, 1975. Genetic variations within and between troops of Macaca fuscata. In "Contemporary Primatology" (S. Kondo, M. Kawai and A. Ehara, ed.). Karger, Basel, pp.75-89.

Nozawa, K., T. Shotake, Y. Ohkura and Y. Tanabe, 1977. Genetic variations within and between species of Asian macaques. Japan. J. Genetics, 52: 15-30.

Nozawa, K., T. Shotake, Y. Kawamoto and Y. Tanabe, in press. Haemotypology and population genetics of Old World monkeys. Proc. XVIIth Cong. Inter. Soc. Haematology, at Paris, 1978.

Ogita, Z., 1966. Genetico-biochemical studies on the salivary and pancreatic amylase isozymes in human. Med. J. Osaka Univ., 16:271-286.

Olivier, T. J., J. Buettner-Janusch and V. Buettner-Janusch, 1974. Carbonic anhydrase isoenzymes in nine troops of Kenya baboons, Papio cynocephalus (Linnaeus, 1766) Am. J. Phys. Anthrop., 41: 175-190.

Omoto, K., S. Harada, T. Tanaka, H. Nigi and W. Prychodko, 1970. Distribution of the electrophoretic variants of serum alpha$_1$-anti-trypsin in six species of the macaques. Primates, 11: 215-228.

Roth, W. T., 1965. The taxonomy of the Baboon and its position in the order of Primates. In "The Baboon in Medical Research" (H. Vagtborg, ed.). Univ. of Texas Press, Vol. 1, pp.3-16.

Scandalios, G., 1964. Tissue specific isozyme variations in maize. J. Hered., 55: 281-285.

Selander, R. K., 1976. Genic variation in natural populations. In "Molecular Evolution" (F. J. Ayala ed.) pp.21-45, Sinauer, Sunderland.

Shaw, C. R. and R. Prasad, 1970. Starch gel electrophoresis of enzymes - a compilation of recipes. Biochem. Genet., 4: 297-320.

Shotake, T., 1974. Genetic polymorphisms of blood proteins in the troops of Japanese macaques, Macaca fuscata. II. Erythrocyte lactate dehydrogenase polymorphism in Macaca fuscata. Primates, 15: 297-303.

Shotake, T., 1978. Genetic differentiation among primtes. Kagaku, 48: 240-246 (in Japanese)

Shotake, T., 1979. Serum albumin and erythrocyte adenosine deaminase polymorphism with special reference to taxonomic relationships among Macaca assamensis, M. radiata and M. mulatta. Primates, 20: 443-451.

Shotake, T., 1980. Genetic variability within and between herds of gelada baboons in central Ethiopian Highland. Antoropologia Conteporanea, 3: 270. (abstract)

Shotake, T. and K. Nozawa, 1974. Genetic polymorphisms of blood proteins in the troops of Japanese macaques, Macaca fuscata I. Cytoplasmic malate dehydrogenase polymorphism in Macaca fuscata, and nonhuman primates. Primates, 15: 219-226.

Shotake, T., K. Nozawa and Y. Tanabe, 1977. Blood protein variation in baboons. I. Gene exchange and genetic distance between Papio anubis, Papio hamadryas and their hybrid. Japan. J. Genetics, 52: 223-237.

Shotake, T. and Y. Ohkura, 1975. Genetic polymorphisms of blood proteins in the troops of Japanese macaques, Macaca fuscata III. Erythrocyte carbonic anhydrase polymorphism in Macaca fuscata. Primates, 16: 17-22.

Shotake, T., Y. Ohkura and K. Nozawa, 1975. A fixed state of the PGM^{2}_{2mac} allele in the population of the Yaku macaque (Macaca fuscata yakui). In "Contemporary Primatology" (S. Kondo, M. Kawai and A. Ehara, ed.), Karger, Basel, pp.67-74.

Shotake, T., Y. Ohkura and G. Ishimoto, 1977. Genetic polymorphisms of blood proteins in the troops of Japanese macaques, Macaca fuscata. V. Erythrocyte phosphohexose isomerase polymorphism. Primates, 18: 281-286.

Sokal, R. R. and P. H. A. Sneath, 1963. Principles of Numerical Taxonomy. Freeman, San Francisco.

Spencer, N., D. A. Hopkinson and H. Harris, 1968. Adenosine deaminase polymorphism in man. Ann. Hum. Genet., 32: 9-14.

Sugawara, K., 1979. Sociological study of a wild group of hybrid baboons between Papio anubis and P. hamadryas in the Awash valley, Ethiopia. Primates, 20: 21-56.

Sugawara, K., in press. Sociological comparison between two wild groups of anubis-hamadryas hybrid baboons. Kyoto University African Studies:

Sugiyama, Y., 1960. On the division of a natural troop of Japanese monkeys at Takasakiyama. Primates, 2: 109-148.

Szalay, F. S. and E. Delson, 1979. Evolutionary history of the

primates. Academic Press, New York and London.

Tappen, N. C., 1960. Problems of distribution and adaptation of the African monkeys. Current Anthropology, I: 91-120.

Wright, S., 1938. Size of population and breeding structure in relation to evolution, Science, 87: 430-431.

Wright, S., 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution, 19: 395-420.

Table 1 Blood samples of baboons in the present work

Ak	(28)	Papio anubis from Kenya
AI	(27)	Papio anubis of Ito troop
AW	(13)	Papio anubis of Welenchiti troop
MG	(18)	Hybrid of Gorge troop
MK	(43)	Hybrid of Kerrayu troop
HBA	(39)	Papio hamadryas of Bassaka A band
HBB	(19)	Papio hamadryas of Bassaka B band
HS	(35)	Papio hamadryas of Sabure Gorge troop
HC	(49)	Papio hamadryas of Cassem Gorge troop
HAG	(292)	Papio hamadryas of Awash Game Reserve troops

Table 2 List of blood proteins examined

Abbreviation	Name of blood protein	Reference
PA-1	Plasma prealbumin-1	Barnicot, Huehns and Dance (1965)
PA-2	Plasma prealbumin-2	Barnicot, Huehns and Dance (1965)
Alb	Plasma albumin	Shotake (1979)
Tf	Plasma transferrin	Barnicot, Huehns and Dance (1965)
Hp	Plasma haptoglobin	Ishimoto (1972)
Pi	Plasma protease inhibitor	Omoto et al. (1970)
α_2	Plasma slow α_2 globulin	Barnicot, Huehns and Dance (1965)
Cp	Plasma ceruloplasmin	Imlah (1964)
Amy	Plasma amylase	Ogita et al. (1966)
Cat	Plasma catalase	Shaw and Prasad (1970)
Ch-Es	Plasma choline esterase	Barnicot, Huehns and Dance (1965)
Plasma Es	Plasma esterase	Barnicot, Huehns and Dance (1965)
Alp	Plasma alkaline phosphatase	Shaw and Prasad (1970)
LAP	Plasma leucin aminopeptidase	Scandalios (1964)
Hb-α	Hemoglobin-α	Ishimoto, Kuwata and Shotake (1975)
Hb-β	Hemoglobin-β	Ishimoto, Kuwata and Shotake (1975)
PHI	Cell phosphohexose isomerase	Shotake, Ohkura and Ishimoto (1977)
6PGD	Cell 6-phosphogluconate dehydrogenase	Ishimoto (1972)
PGM-I	Cell phosphoglucomutase-I	Shotake, Ohkura and Nozawa (1975)
PGM-II	Cell phosphoglucomutase-II	Shotake, Ohkura and Nozawa (1975)
ADA	Cell adenosine deaminase	Spencer, Hopkinson and Harris (1968)
Dia	Cell NADH-diaphorase	Ishimoto (1972)
CA-I	Cell carbonic anhydrase-I	Shotake and Ohkura (1975)
CA-II	Cell carbonic anhydrase-II	Tashian et al. (1972)
Acp	Cell acid phosphatase	Ishimoto (1972)
G6PD	Cell glucose-6-phosphate dehydrogenase	Shaw and Prasad (1970)
MDH	Cell malate dehydrogenase	Shotake and Nozawa (1974)
LDH-A	Cell lactate dehydrogenase-A	Shotake (1974)
LDH-B	Cell lactate dehydrogenase-B	Shotake (1974)
TO	Cell tetrazolium oxidase	Baur and Schorr (1969)
IDH	Cell isocitrate dehydrogenase	Ishimoto, Kuwata and Shotake (1974)
AK	Cell adenylate kinase	Shaw and Prasad (1970)
EsD	Cell esterase D	Hopkinson et al. (1973)
Cell Es	Cell esterase	Kitajima et al. (1975)

Table 3. Allele frequencies of variable protein loci in the baboon populations

Locus and allele		Baboon population									
		AK	AI	AW	MG	MK	HBA	HBB	HS	HC	HAG
Tf	D	0	0	0.0385	0.1389	0.1628	0.1538	0.0789	0.0571	0.1122	0.1182
	D'	1.0000	0.8846	0.8846	0.6667	0.2907	0.0257	0.0789	0.0714	0.1122	0.0839
	E	0	0.0769	0.0769	0.1667	0.5462	0.8205	0.8421	0.8714	0.7755	0.7979
	C	0	0.0385	0	0.0278	0	0	0	0	0	0
Pi	P	1.0000	1.0000	1.0000	0.9444	0.9884	1.0000	0.8947	0.9714	0.9898	0.9552
	Q	0	0	0	0.0556	0	0	0.1053	0	0	0.0431
	N	0	0	0	0	0.0116	0	0	0.0286	0.0102	0.0017
PA-2	1	0	0.0192	0.1923	0.0556	0.6395	0.8205	0.7353	0.7429	0.8470	0.6573
	2	1.0000	0.9808	0.8077	0.9444	0.3256	0.0897	0.1765	0.2571	0.1224	0.2780
	3	0	0	0	0	0.0349	0.0897	0.0882	0	0.0306	0.0647
Plasma Es	F	0	0	0	0.3333	0.3023	0.2679	0.1944	0.5429	0.4796	0.4739
	S	1.0000	1.0000	1.0000	0.6667	0.6977	0.7321	0.8056	0.4571	0.5204	0.5261
6PGD	E	1.0000	1.0000	1.0000	0.9722	0.8953	0.8846	0.7895	0.9571	0.9490	0.9633
	F	0	0	0	0.0278	0.1047	0.1154	0.2105	0.0429	0.0510	0.0367
PGM-1	4	1.0000	0.8462	0.8462	0.7500	0.9651	1.0000	1.0000	1.0000	1.0000	1.0000
	5		0.1538	0.1538	0.2500	0.0349	0	0	0	0	0
PGM-II	3	1.0000	1.0000	0.8077	0.8889	1.0000	1.0000	1.0000	1.0000	1.0000	0.9913
	4	0	0	0.1923	0.1111	0	0	0	0	0	0.0087
ADA	2	0.6786	0.8462	1.0000	1.0000	0.9884	1.0000	1.0000	0.9714	0.9490	0.9843
	4	0.3214	0.1538	0	0	0.0116	0	0	0.0286	0.0510	0.0157
CA-I	a	0.9286	1.0000	0.9231	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.9739
	b	0.0714	0	0.0769	0	0	0	0	0	0	0.0261
AK	1	1.0000	0.8846	1.0000	1.0000	1.0000	0.9872	1.0000	0.9429	0.9592	0.9912
	2	0	0.1154	0	0	0	0.0128	0	0.0571	0.0408	0.0088

Table 4 Quantification of genetic variability and hybridization of baboon populations

	P_{poly}	$\bar{H} = 1-\overline{\sum q_i^2}$	$n_e = 1/\overline{\sum q_i^2}$	hybridization[1] rate	
AK	2/34 = 0.0588	0.0167	1.0170		
AI	5/34 = 0.1471	0.0286	1.0294		
AW	5/34 = 0.1471	0.0363	1.0377	0.7433	
MG	7/34 = 0.2059	0.0526	1.0555	0.7537	(0.6179)[2]
MK	7/34 = 0.2059	0.0529	1.0559	0.3286	(0.2245)
HBA	5/34 = 0.1471	0.0363	1.0377	0.0290	
HBB	5/34 = 0.1471	0.0451	1.0472	0.0314	
HS	7/34 = 0.2059	0.0415	1.0433	0.0807	
HC	7/34 = 0.2059	0.0421	1.0440	0.1268	
HAG	7/34 = 0.2059	0.0471	1.0494	0.0948	

1) penetration rate of anubis genes

2) the figures in parentheses are the average of three loci, Tf, PA-2 and Es

Table 5 Matrices of genetic distance (D) under the diagonal and genetic similarity (I) above the diagonal between every pair of baboon populations. The figures in parentheses are genetic distances corrected by hybridization rate.

	AK	AI	AW	MG	MK	HBA	HBB	HS	HC	HAC
AK		0.9976	0.9935	0.9885	0.9682	0.9465	0.9516	0.9468	0.9468	0.9531
AI	0.0024		0.9964	0.9936	0.9713	0.9538	0.9586	0.9540	0.9532	0.9596
AW	0.0065	0.0036		0.9942	0.9794	0.9615	0.9655	0.9597	0.9602	0.9676
MG	0.0116	0.0064	0.0058		0.9823	0.9640	0.9672	0.9683	0.9697	0.9723
MK	0.0323	0.0291	0.0208	0.0179		0.9967	0.9967	0.9936	0.9962	0.9972
HBA	0.0550 (0.0583)	0.0473 (0.0503)	0.0393 (0.0774)	0.0367	0.0034		0.9989	0.9966	0.9977	0.9974
HBB	0.0496 (0.0541)	0.0423 (0.0451)	0.0351 (0.0688)	0.0334	0.0033	0.0011		0.9948	0.9959	0.9962
HS	0.0546 (0.0790)	0.0471 (0.0546)	0.0411 (0.0933)	0.0322	0.0064	0.0034	0.0052		0.9992	0.9994
HC	0.0546 (0.0719)	0.0479 (0.0684)	0.0406 (0.1064)	0.0308	0.0038	0.0023	0.0041	0.0008		0.9991
HAG	0.0480 (0.0582)	0.0413 (0.0505)	0.0329 (0.0830)	0.0281	0.0028	0.0026	0.0038	0.0006	0.009	

Table 6 Morphological (M.I.A.) and Genetical Indices (G.I.A.) of anubis, Behavioural Rank Order (B.R.O.) and correlation coefficients among three genotypes between M.I.A. and G.I.A. and between B.R.O. and rank order of M.I.A.

Name*		M.I.A*	B.R.O*	G.I.A.			
				Tf	Es	PA-2	Total
Gorge group							
Matiou	Adult ♂	16	6	CD' (2.0)	FS(0.5)	2-2(1.8)	4.3
Louis	Adult ♂	16	7	D'E (1.0)	SS(1.0)	2-2(1.8)	3.8
Maler	Adult ♂	15	2	DD (0)	SS(1.0)	2-2(1.8)	2.8
Mirabeau	Adult ♂	14	8	D'D'(2.0)	FF(0)	2-2(1.8)	3.8
Baboof	Adult ♂	13	3	D'D'(2.0)	FS(0.5)	2-2(1.8)	4.3
Necker	Adult ♂	13	4	D'E (1.1)	FF(0)	2-2(1.8)	2.9
Green	Adult ♂	12	5	D'D'(2.0)	SS(1.0)	2-2(1.8)	4.8
Hagos	Adult ♂	3	1	DD (0)	FF(0)	2-2(1.8)	1.8
Kerrayu group							
Doro	Adult ♂	9	4	ED' (1.1)	FS(0.5)	1-2(0.9)	2.5
Feres	Adult ♂	8	9	ED (0.1)	SS(1.0)	1-1(0)	1.1
Zefen	Adult ♂	6	3	ED' (1.1)	FF(0)	1-1(0)	1.1
Igir	Adult ♂	6	10	D'D'(2.0)	FF(0)	1-2(0.9)	2.9
Djoro	Adult ♂	6	10	EE (0.2)	FF(0)	1-1(0)	0.2
Jirat	Adult ♂	5	6	D'D'(2.0)	FS(0.5)	2-2(1.8)	4.3
Kusil	Adult ♂	4	7	DD (0)	FS(0.5)	2-2(1.8)	2.3
Posta	Adult ♂	3	8	ED' (1.1)	FS(0.5)	2-2(1.8)	3.4
Yabelo	Adult ♂	2	2	ES' (1.1)	SS(1.0)	1-2(0.9)	3.0
Stav	Adult ♂	2	5	DD' (1.0)	FS(0.5)	1-1(0)	1.5
Geta	Adult ♂	2	1	EE (0.2)	SS(1.0)	2-2(1.8)	3.0

I. Correlation coefficients among three genotypes

Gorge group (n = 18)
- Tf & Es r = 0.0361 0.1 < p
- Tf & PA r = -0.0616 0.1 < p
- Es & PA r = 0.1344 0.1 < p

Kerrayu group (n = 43)
- Tf & Es r = -0.176 0.1 < p
- Tf & PA r = 0.010 0.1 < p
- Es & PA r = 0.002 0.1 < p

II. Correlation coefficients between G.I.A. and M.I.A. in adult males

Gorge group (n = 8)
1. Tf & M.I.A. r = 0.4429 0.1 < p
2. PA & M.I.A. r = 0. 0.1 < p
3. Es & M.I.A. r = 0.4141 0.1 < p
4. G.I.A.(Total) & M.I.A. r = 0.6193 0.1 < p

Kerrayu group (n = 11)
1. Tf & M.I.A. r = -0.3601 0.1 < p
2. PA & M.I.A. r = -0.3663 0.1 < p
3. Es & M.I.A. r = -0.4229 0.1 < p
4. G.I.A.(Total) r = -0.3228 0.1 < p

III. Rank correlations between B.R.O. and rank order of G.I.A.

Gorge group (n = 8)
r = 0.4762 0.1 < p

Kerrayu group (n = 11)
r = -0.1954 0.1 < p

* Cited from Sugawara (1979, in press). For detailed explanation see the text.

Table 7 Age-sex compositions of Bassaka hamadryas troop and estimation of effective population size in January 1976.

Band or troop	Adult males	Adult and subadult females	Subadult males	Youngs to 3 years old	N_c	$\sum_i k_{mi}^2$ [2]	N(N) [3]	N(W) [4]
HB-A band	14(8) [1]	20	8	28	70	64	40	33
HB-B band	9(5)	12	4	20	45	32	25	21
HB-troop	23(13)	32	12	48	115	96	66	54

1) The figures in parentheses give the number of leader males with units
2) Sum of square of the number of females in one male units
3) Effective population size estimated by Nozawa's formula
4) Effective population size estimated by Wright's formula

Table 8 Estimation of migration rate ($\bar{m}$ per generation) between neighboring bands and troops of the hamadryas baboons and between neighbouring hybrid and anubis groups

Group of troops (Census size)	Variable locus	Commonest allele	Allele frequency q			$\bar{q}$	σ_q^2	F_{ST}	$\overline{F_{ST}}$	$\bar{N}$	$\bar{m}$
			HBA	HBB							
	Tf	E	0.8205	0.8421		0.8313	0.000090	0.000642			
HBA (70)	Pi	P	1.0	0.8947		0.9474	0.002778	0.055750			
	PA-2	1	0.8205	0.7353		0.7779	0.001822	0.010546			
HBB (45)	P-Es	S	0.7321	0.8056		0.7689	0.001370	0.007710			
	6PGD	E	0.8846	0.7895		0.8371	0.002247	0.016478			
	AK	1	0.9872	1.0		0.9936	0.000059	0.004277	0.015901	27	0.317
			HB	HS							
	Tf	E	0.8276	0.8714		0.8495	0.002700	0.021127			
HB (115)	Pi	P	0.9655	0.9714		0.9685	0.000005	0.000163			
	PA-2	1	0.7946	0.7429		0.7688	0.000650	0.003656			
HS (150)	P-Es	S	0.7895	0.4571		0.6233	0.055200	0.234893			
	6PGD	E	0.8534	0.9571		0.9053	0.002650	0.030886			
	ADA	2	1.0	0.9714		0.9857	0.000195	0.013830			
	AK	1	0.9914	0.9429		0.9672	0.000600	0.018868	0.046199	65	0.071
			HS	HC							
	Tf	E	0.8714	0.7755		0.8235	0.002300	0.015821			
HS (150)	Pi	P	0.9714	0.9898		0.9806	0.000084	0.004416			
	PA-2	1	0.7429	0.8470		0.7950	0.002705	0.016597			
HC (150)	P-Es	S	0.5429	0.4796		0.5113	0.010030	0.004014			
	6PGD	E	0.9571	0.9490		0.9531	0.000015	0.000336			
	ADA	2	0.9714	0.9490		0.9602	0.000126	0.003293			
	AK	1	0.9429	0.9592		0.9511	0.000064	0.001375	0.006550	75	0.293
			HB	HS	HC						
	Tf	E	0.8276	0.8714	0.7755	0.8248	0.001533	0.010609			
HB (115)	Pi	P	0.9655	0.9714	0.9898	0.9756	0.000100	0.004202			
	PA-2	1	0.7946	0.7429	0.8470	0.7948	0.001800	0.011036			
HS (150)	P-Es	S	0.7895	0.4571	0.5204	0.5890	0.020733	0.085682			
	6PGD	E	0.8534	0.9571	0.9490	0.9198	0.002200	0.029810			
HC (150)	ADA	2	1.0	0.9714	0.9490	0.9735	0.000433	0.016795			
	AK	1	0.9914	0.9429	0.9592	0.9645	0.000433	0.012670	0.024401	68	0.120
			MG	MK							
	Tf	D'	0.6667	0.2907		0.4787	0.035350	0.141650			
	Pi	P	0.9444	0.9884		0.9664	0.000480	0.014780			
MG (63)	PA-2	2	0.9444	0.3256		0.6350	0.095730	0.413030			
	P-Es	S	0.6667	0.6977		0.6822	0.000240	0.001107			
MK (85)	6PGD	E	0.9722	0.8953		0.9338	0.014800	0.023940			
	PGM-I	4	0.7500	0.9651		0.8576	0.011570	0.094740			
	PGM-II	3	0.8889	1.0		0.9445	0.003090	0.058950			
	ADA	2	1.0	0.9884		0.9942	0.000030	0.000570	0.093596	29	0.075
			AI	MG							
	TF	D'	0.8846	0.6667		0.7757	0.011867	0.068201			
	Pi	P	1.0	0.9444		0.9722	0.000777	0.028778			
	PA-2	2	0.9808	0.9444		0.9626	0.000351	0.009750			
AI (60)	P-Es	S	1.0	0.6667		0.8334	0.027975	0.202132			
	6PGD	E	1.0	0.9722		0.9861	0.000207	0.015109			
MG (63)	PGM-I	4	0.8462	0.7500		0.7981	0.002336	0.014500			
	PGM-II	3	1.0	0.8889		0.9445	0.003064	0.058473			
	ADA	2	0.8462	1.0		0.9231	0.005936	0.083606			
	AK	1	0.8846	1.0		0.9423	0.003321	0.061048	0.060177	21	0.138

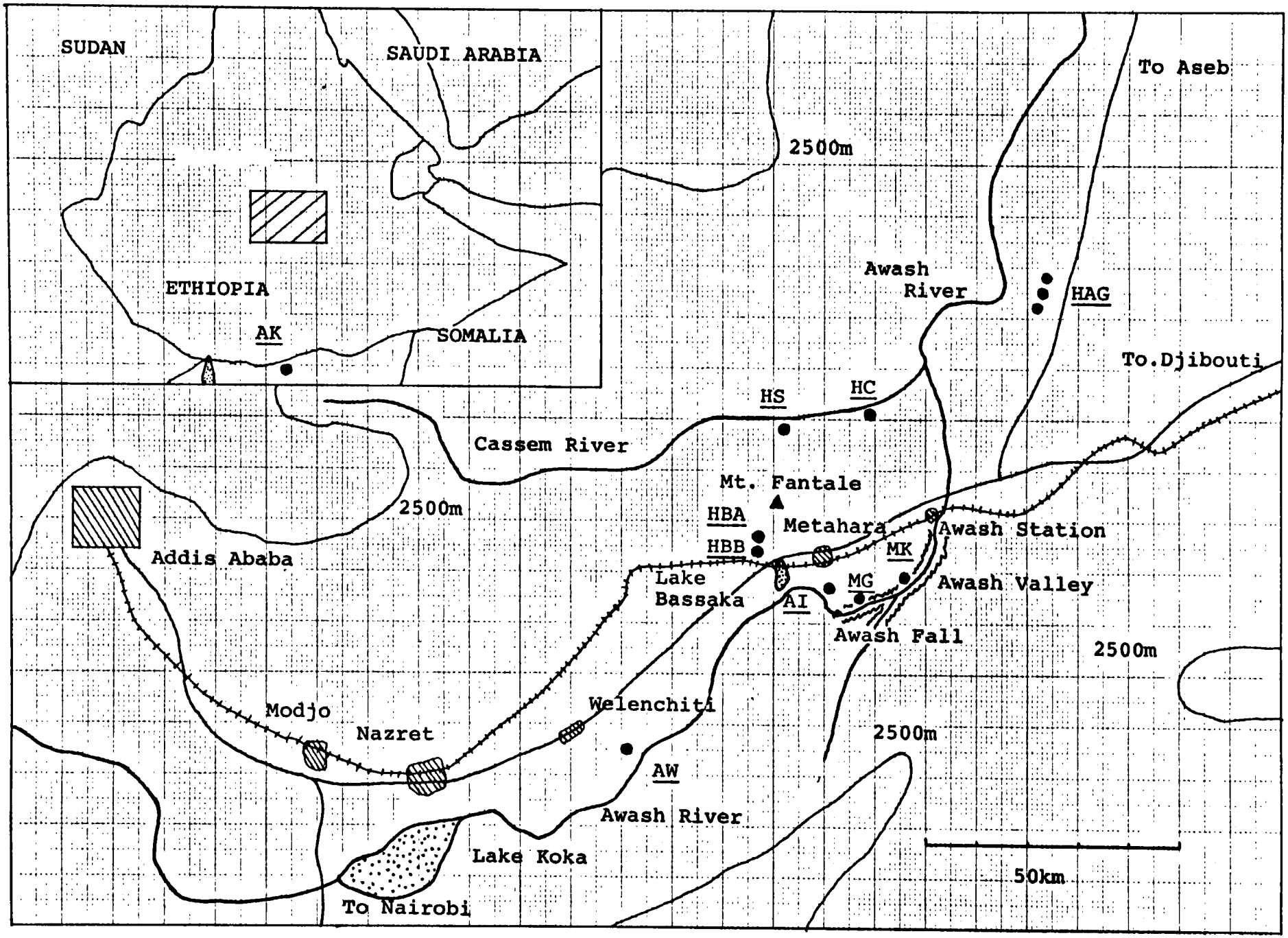
Legend

Fig. 1 Location of populations from which the blood samples were collected in central Ethiopia.

Fig. 2 Zymogram of electrophoretic variant phenotypes found in this work.

Fig. 3 Dendrogram drawn from the Nei's genetic distance (D) among baboon populations.

Fig. 1


SUDAN
SAUDI ARABIA
To Aseb
2500m
ETHIOPIA
Awash
River
HAG
AK
SOMALIA
To.Djibouti
HS
HC
Cassem River
Mt. Fantale
2500m
HBA
Metahara
Awash Station
Addis Ababa
HBB
MK
Lake
Bassaka
MG
Awash Valley
AI
Awash Fall
2500m
Modjo
Welenchiti
Nazret
2500m
AW
Awash River
Lake Koka
50km
To Nairobi

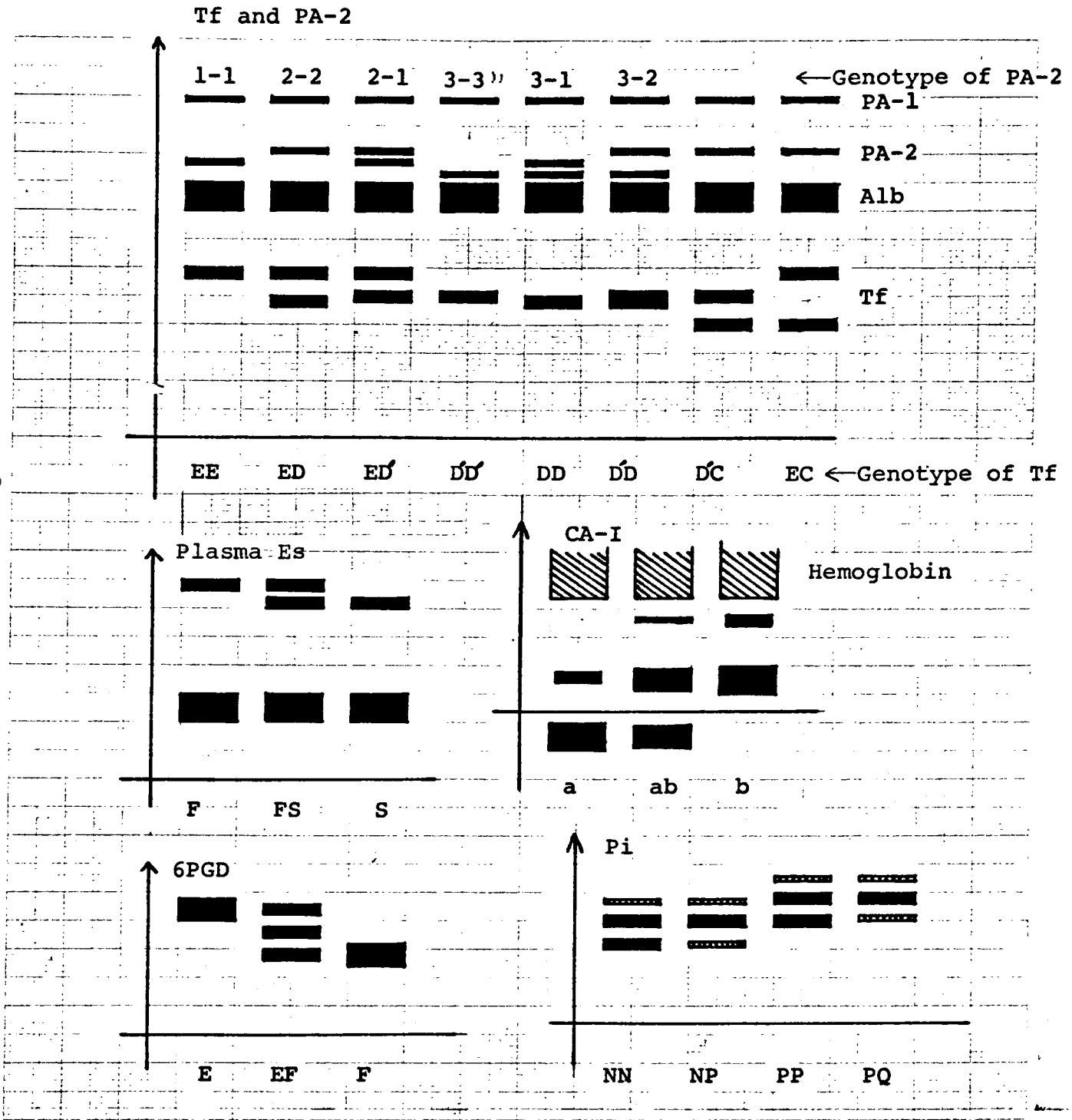

Tf and PA-2
1-1
2-2
2-1
3-3
3-1
3-2
←Genotype of PA-2
PA-1
PA-2
Alb
Tf
EE
ED
ED'
D'D'
DD
D'D
D'C
EC ←Genotype of Tf
Plasma Es
F
FS
S
CA-I
Hemoglobin
a
ab
b
6PGD
E
EF
F
Pi
NN
NP
PP
PQ

Fig. 2

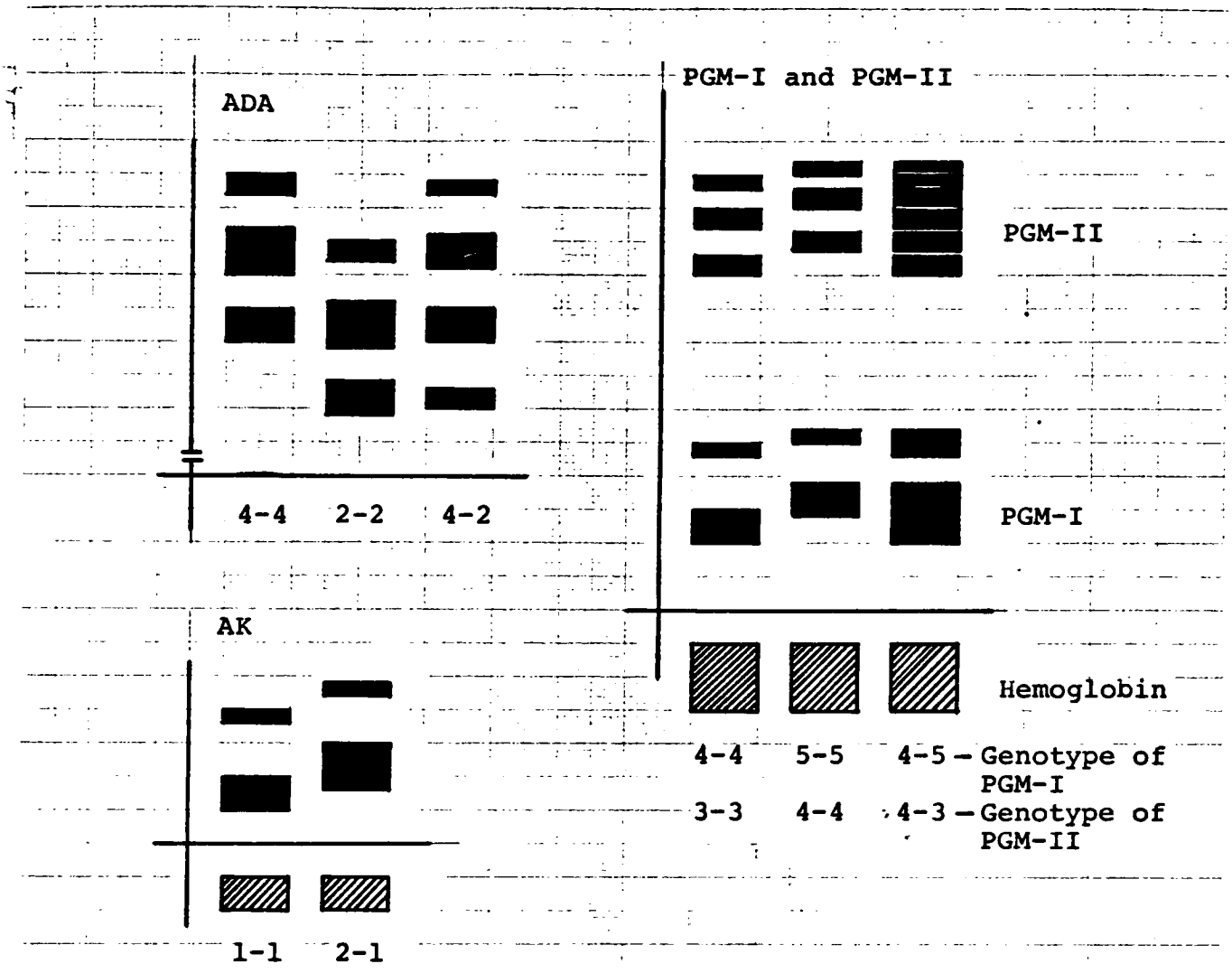
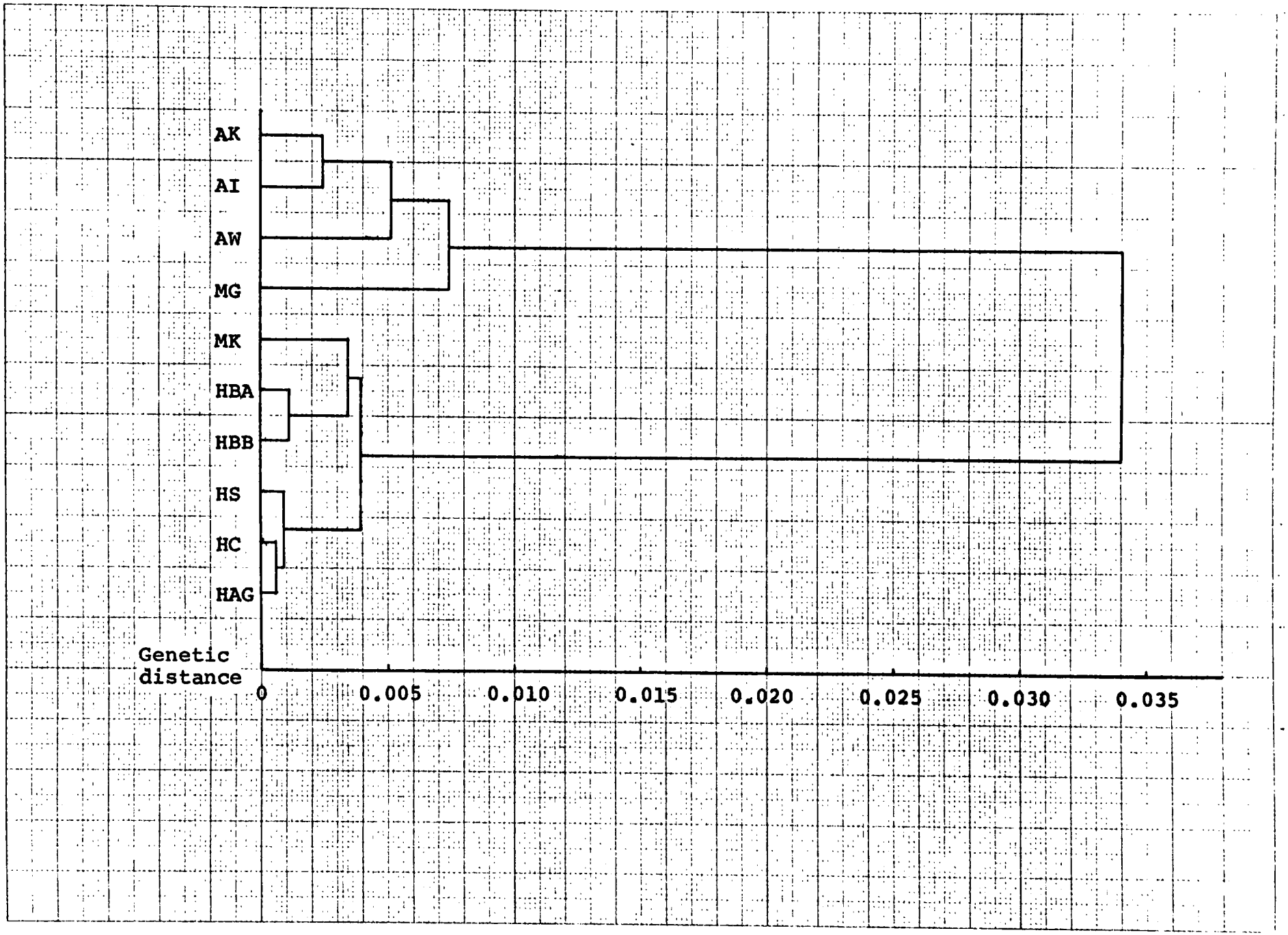

ADA
4-4
2-2
4-2
AK
1-1
2-1
PGM-I and PGM-II
PGM-II
PGM-I
Hemoglobin
4-4
5-5
4-5 – Genotype of PGM-I
3-3
4-4
4-3 – Genotype of PGM-II

Fig. 2

ig. 3


AK
AI
AW
MG
MK
HBA
HBB
HS
HC
HAG
Genetic distance
0
0.005
0.010
0.015
0.020
0.025
0.030
0.035